Grama (*Bouteloua* Lag.) Communities in a Southeastern Arizona Grassland

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Highlight: Fifty stands, representing six common and three rare species of gramas (genus *Bouteloua*), were sampled for vegetation abundance, species composition, and selected habitat factors. Numerical and statistical procedures were used to aid in obtaining succinct descriptions of the habitat structure of the grama species. Factors such as texture and content of various nutrients of the soils were among those that showed trends.

Black grama (*B. eriopoda*) was found to be associated with soils higher in nitrate, potassium, organic matter, pH, and lime. Most similar to stands of black grama were stands of eludens grama (*B. eludens*) and sideoats grama (*B. curtipendula*), which tended to also be associated with sandy clay textured soils and steep, rocky slopes. All stands of eludens grama were found on southerly exposures. Hairy grama (*B. hirsuta*) and spruce-top (*B. chondrosiodes*) were most widely distributed and tended to occur together on relatively level sites with clayey, acidic soils. Curly mesquite (*Hilaria belangeri*) was nearly always associated with these two gramas. Blue grama (*B. gracilis*) tended to be most abundant on acidic, relatively infertile, sandy clay loam soils.

The grama grasses (*Bouteloua* species) are the single most important group of perennial grasses in southern Arizona, not only in terms of abundance but economics. According to Humphrey (1958), the gramas constitute the major portion of the range forage in this region and consequently they are managed for maximum production in preference to many other grass species.

The objective of this study was to generate hypotheses about the habitat structure of the six important species of grama within the boundary of a southeastern Arizona study area. Structural characterization included the description of habitat characteristics where the species occurred. Physical and chemical soil attributes were the primary abiotic factors considered in the structural descriptions. Other plant species that consistently occurred within the grama communities were the most useful and easily measured biotic component.

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Description of Area

All samples were taken within the boundaries of The Research Ranch, Inc., located 9.6 km south of Elgin, Santa Cruz County, Arizona. The total area of the ranch is approximately 30 km². Elevation ranges from 1,618 m at the northeastern corner to 1.774 m at the southern boundary. The northern half of the study area is characterized by narrow ridges and steeply sloping canyons. The relief in this portion may be as much as 35 m, with slopes as steep as 35 degrees. The southern half of the study area consists of small plateaus that are deeply dissected into narrow, steep-walled canyons. Relief in this area ranges up to 70 m, with slopes as steep as 35 degrees.

The vegetation is predominantly perennial grasses; gramas and threeawns (*Aristida* species) along with wolftail (*Lycurus phleoides*) are the most important. Dense stands of alkali sacaton (*Sporobolus airoides*) are found on most flood plains. In the northern part of the study area, oaks (*Quercus* species) are found only on north-facing slopes, while in the southern portion at higher elevations oaks are important on all exposures. Oaks also form some savannah-like areas.

Methods and Procedures

Fifty vegetation stands were sampled in August and September, 1971. Stand boundaries were established to delineate homogenous grama types with respect to the most abundant grama species occurring within the stand. Nine species are endemic to the study area, while only six are commonly encountered. Consequently, out of the 50 stands, 45 were of the common species type.

Initially, a species list was made as an index of species richness. Frequency (quadrats of occurrence/total quadrats × 100) was determined for each species in each stand. Eighty 40 × 40-cm quadrats were located at regular intervals throughout each vegetation stand. The first quadrat location was selected at random and the remainder of the quadrats were spaced at equal intervals to insure that all portions of the stand were represented in the 80 samples. Basal cover was estimated by classes for all graminoid species by locating an additional 24 40 × 40-cm quadrats in each stand. Six cover classes were utilized:

(i) 0–5%; (ii) 6–25%; (iii) 26–50%; (iv) 51–75%; (v) 76–95%; (vi) 96–100%. Mid-points of the class interval were used to compute means for each species in each stand.

The degree of the slope and angle of exposure for each stand was measured. Elevation was estimated from 50-foot contour intervals on a U.S. Geological Survey Map.

A composite soil sample from the surface 6 inches was obtained from five subsamples taken at regular locations in each stand. The soil samples were first sieved to determine percentage rock (by mass) of five particle size classes: all rocks greater than 2 mm; this was further subdivided into 2–4 mm, 5–14 mm, 15–30 mm, and greater than 30 mm. The remainder of the sample (less than 2 mm) was mechanically analyzed for texture using the hydrometer method. Percent soil water (by mass) at zero bars water potential was determined by a modification of the Hilgard (1906) method.

Standard procedures were used to determine pH, percent lime, soluble salts (electrical conductivity), percent organic matter, available phosphorus, potassium, nitrate-nitrogen, zinc, and iron, and percent water at ⅓ and 15 bars soil water potential.

Assuming we encountered about 35 species per stand, the above procedures resulted in 1,750 individual frequency and 1,750 cover observations for the 50 stands. The 24 habitat factors measured resulted in 1,200 individual observations. Such large data matrices cannot be synthesized by casual inspection. Therefore, we chose to utilize three numerical methods, which would reduce the original data matrices into relevant and succinct descriptions: correlation, regression, and phytosociological ordination.

Product-moment correlation coefficients were computed between all habitat factors and the 18 most frequent species themselves (Nicholson 1972). However, only the grama species vs habitat factor correlations will be presented herein. Coefficients greater than 0.36 were significantly different than zero at $P = 0.05$ level (Rohlf and Sokal 1969). All correlations that are mentioned hereafter were significant at least at the $P = 0.05$ level.

A stepwise multiple regression was also used as an aid in determining cognate habitat variables. The general multiple regression formula was:

$$Y = a + b_1x_1 + b_2x_2 + \ldots + b_ix_i \quad (1)$$

where a is a constant, $b_1, b_2, \ldots b_i$ are the regression coefficients on the independent variables $x_1, x_2, \ldots x_i$ selected. The frequencies of the six most common grama species were the dependent variables. Regressions with independent variables consisting of habitat factors were calculated separately from those using the frequencies of 12 associated species. To choose the number of independent variables, the multiple coefficient of correlation, the standard error of the estimate, and the partial F ratios were used. The assumption was made that the resultant independent variables chosen were those that would be most likely associated with the gramas.

Ordination procedures of Swan et al. (1969) were used in this study. Interstand distances were computed for each stand-pair combination according to the Euclidean formula:

$$d = [\Sigma (x_{ni} - x_{nj})^2]^{1/2} \quad (1)$$

where x_n are values of the variables 1 through n; and i and j are the two stands involved in the pair-combination. Values used to order all stands on all possible stand-pair defined x axes are computed according to the formula:

$$alpha = \frac{d^2_{AB} + d^2_{AP} - d^2_{BP}}{2d_{AB}} \quad (2)$$

where d= interstand distance, A and B are the two stands defining the axis, and P is the stand being located. The best possible axis is then selected by using the stand-pair with the greatest mSS_a where:

$$mSS_a = m\Sigma(a-\bar{a})^2 = m\Sigma a^2 - (\Sigma a)^2 \quad (3)$$

with $m = 50$ (number of stands) and SS_a = the sum of squares of the interstand distances along the x-axis. Subsequent axes were selected from the residuums of the nonperfect fit of the stands on the best preceding axis.

Greig-Smith (1964) recommended that variables having greatly differing magnitudes of absolute value (such as elevation and organic matter percentage) should be relativized for this type of ordination so that no one variable has an undue amount of influence upon ordinal stand locations. Each variable was first summed over the entire 50 stands, then each value for that variable, resulting in a relative value for each of the variables in each stand. Frequency values did not need to be transformed since they are inherently relative and within the same range of variability as the transformed habitat values.

The computer program SDW∅RD (Hoag 1971) was used to compute coordinates on three axes for the 50 vegetation stands. Different sets of variables were used resulting in four partial ordinations and one ordination in which all variables were utilized: (A)

Table 1. Mean values for all quantitative habitat factors in 45 stands. Stands included in each grama group were those with the highest percent basal cover.

	Grama groups						
Factors	Spruce-top	Sideoats	Eludens	Black	Blue	Hairy	Mean
Sand (%)	37.3	51.7	50.8	41.2	54.1	41.6	45.6
Silt (%)	18.0	12.4	12.8	19.7	17.5	15.2	16.0
Clay (%)	44.6	35.8	36.2	39.0	28.2	43.1	38.2
>2 mm rock (%)	34.4	56.7	61.8	50.2	21.4	41.0	43.7
2–4 mm rock (%)	5.7	9.2	11.5	7.1	9.4	6.6	8.1
5–14 mm rock (%)	11.2	18.4	20.4	12.4	6.8	11.1	13.2
15–30 mm rock (%)	10.1	15.4	14.8	10.7	2.7	11.5	10.8
>30 mm rock (%)	7.3	13.4	15.0	20.0	2.4	11.6	11.4
0 bar (% soil H_2O)	54.7	49.9	49.2	56.6	40.6	54.3	51.1
⅓ bar (% soil H_2O)	21.0	16.1	16.8	22.1	13.2	19.3	18.2
15 bar (% soil H_2O)	14.5	11.1	12.0	14.5	8.0	13.2	12.3
Slope (degrees)	4.2	15.4	19.7	3.4	2.2	4.7	8.0
Elevation (feet)	4900.0	4835.0	4810.0	4807.0	4832.0	4878.0	4847.0
Mean no. species	30.5	39.0	27.1	32.1	43.1	37.5	34.7
Total no. stands	9	7	7	7	7	8	7
pH	6.0	7.0	7.7	7.8	6.2	5.8	6.7
Salts (mmohs)	0.3	0.4	0.3	0.4	0.3	0.2	0.3
Organic matter (%)	1.8	1.7	1.8	2.1	1.1	1.9	1.7
Available P (ppm)	4.1	3.4	5.4	6.6	9.2	3.4	5.2
Available K (ppm)	231.8	236.4	139.8	128.2	192.4	261.2	201.2
Available NO_3 (ppm)	1.4	5.2	1.1	4.9	3.4	1.5	2.8
Available Zn (ppm)	1.2	1.0	0.4	0.4	0.9	1.0	0.8
Available Fe (ppm)	12.8	12.1	4.5	3.3	18.6	14.9	11.2

frequency values of all species averaging greater than 10%, (B) all measured physical habitat factors, (C) all measured chemical (soil) habitat factors, (D) B and C combined, (E) A, B, and C combined. Only the first two axes of the five ordinations were used due to the difficulty of portraying graphs in three dimensions and the fact that the first two axes account for most interstand distances.

Results and Discussion

Of the 50 stands, 45 were assigned to one of six categories, using the grama species with the largest percent basal cover as the criterion for selection (Table 1). The remaining five stands had one of the three other species as the most abundant grama.

Mean percentage frequency for all species having an overall mean frequency greater than 10% and the grand mean for all stands were computed (Table 2). These were considered the most important species and were then utilized in subsequent detailed analysis to determine which associated species were most important in the habitats of the gramas.

Table 2. Mean frequencies of the six grama species. Each grama group was composed of the set of stands having the greatest percent basal cover for the said grama species. P = <0.5 percent mean frequency.

	Grama groups						
Grama species	Spruce-top	Side-oats	Eludens	Black	Blue	Hairy	Mean
Spruce-top grama	91	12	16	9	11	62	37
Sideoats grama	1	91	55	25	4	9	29
Eludens grama	0	0	89	14	P	0	16
Black gama	P	5	46	83	20	P	24
Blue grama	5	15	P	3	78	3	16
Hairy grama	37	16	9	16	5	83	29
No. of stands	9	7	7	7	7	8	

Correlation Analysis

Caution should be exercised in interpreting correlation coefficient significance levels in plant-environment relationship studies, since the procedures used herein could, for example, be used to characterize the habitats of utility poles. However, where habitat factors cannot be subjected to control by the experimenter it is a convenient method of first approximation (Sokal and Rohlf 1969).

Grama-Physical Habitat Correlations

Spruce-top grama (*Bouteloua chondrosioides*) and hairy grama (*Bouteloua hirsuta*) were negatively associated with slope (Table 3), indicating that these two species were less important on steeper slopes and more important on flatter sites. However, in the Great Plains, Hulett et al. (1968) reported that hairy grama expressed its greatest importance on steep slopes. Spruce-top grama was more important at the higher elevations on the present study site, which was most likely a function of the general broad topographic effects of Bald Hill, not elevation alone. Nearly the entire northern one-half of the study area is dominated by this important topographic feature.

Of all species, eludens grama (*Bouteloua eludens*) had the highest mean value for slope, (19.7 degrees) for the sites upon which it occurred (Table 1). The fact that it occurred on so few of the 50 stands probably accounts for the low correlation between this species and slope (Table 3). Exposure for eludens grama was limited to a range of 85 through 240 degrees (Nicholson 1972).

In contrast, sideoats grama (*Bouteloua curtipendula*) showed a positive slope association with a mean slope of 15.4 degrees. Dix (1968) also found sideoats grama to be associated with steep slopes in the North Dakota badlands, as did Hulett et al. (1968) in the central Great Plains. This phenomenon was easily observed in the field, where sideoats grama reached its prominence on the steeper slopes of the study area. A positive and probably real correlation was also found between sideoats grama and the 2 to 4-mm rock fraction (Table 3). Results of a study in the central Great Plains were in accord with the correlation between this species and surface rock (Nicholson and Hulett 1969).

Table 4. Correlation coefficients ($r \times 100$) computed between chemical habitat factors and the six grama species. Each grama group was composed of the set of stands having the greatest percent basal cover for the said grama species.

Grama species	pH	Salts	O.M.*	P	K	NO_3	Zn	Fe
Spruce-top grama	−35**	−06	−03	−09	−23	+24	+05	+25
Sideoats grama	+33	−03	−13	+13	−12	−24	−22	−22
Eludens grama	+12	+15	+19	−01	+02	+21	+12	−09
Black grama	+14	+04	−03	+11	−10	+33**	−14	−16
Blue grama	+18	−04	−07	−12	−08	−41***	−09	−20
Hairy grama	−16	−13	−17	−02	00	+05	+10	+16

* Organic matter.
** Coefficients significantly different than zero (p = 0.05).
*** Coefficients significantly different than zero (p = 0.01).

Grama-Chemical Habitat Correlations

As soil pH increased so did the abundance of sideoats grama (Table 4). Spruce-top grama, on the other hand, reacted negatively with pH. Linnell (1961), in an investigation in western Kansas, demonstrated that sideoats grama was the most important species on the more alkaline soils of that region.

Black grama (*Bouteloua eriopoda*) was more important on sites where nitrates were more available, which implies that this species distribution could be dependent upon higher nitrate levels. Blue grama showed an opposite relationship in that it was more abundant on sites where nitrates were less available.

Coefficients of correlation between habitat factors and the remaining 12 of the 18 most important species were also computed (Nicholson 1972). It was noted from the correlation

Table 3. Correlation coefficients ($r \times 100$) computed between physical habitat factors and the six grama species. Each grama group was composed of the set of stands having the greatest percent basal cover for the said grama species.

	Soil particles			Percentage rock					Soil water					
Grama species	Sand	Silt	Clay	>2 mm	2–4 mm	5–14 mm	15–30 mm	>30 mm	0 bar	1/3 bar	15 bar	Slope	Elev.	# spp.
Spruce-top grama	+12	+12	−18	−08	−03	−07	−13	+01	−08	−04	−10	−34*	+56**	+05
Sideoats grama	−11	+10	+05	+13	+29*	+20	+06	−04	−06	+09	00	+32*	−06	−13
Eludens grama	+11	+08	−14	+10	−07	+10	−08	+19	+04	−04	00	+04	−01	+16
Black grama	+01	−09	+02	−03	+04	+11	+09	−21	−01	00	+01	+02	−02	−25
Blue grama	−04	+11	−01	−26	+09	−21	−20	−18	−01	+05	00	−06	−24	−18
Hairy grama	+13	+06	+16	−27	+01	−30*	−11	−19	00	+10	+03	−33*	−07	−12

* Coefficients significantly different than zero (p = 0.05).
** Coefficients significantly different than zero (p = 0.01).

matrices that the 12 associated species appeared to be more closely associated with the habitat factors measured than were the six grama species. Associated species were significantly correlated with 30% of all the habitat factors. Two-thirds of those significant correlations were significant at a probability of at least $P = 0.01$, while the remaining ⅓ were significant at a probability of at least $P = 0.05$. The grama species were significantly correlated with only 7% of all habitat factors (as compared to 30% above). Six of the 7% were significant at least at the $P = 0.05$ level, and the remaining 1% of the significant correlations were significant at least at the $P = 0.01$ level. This was probably because the site samples were selected upon the basis of having an abundance of one or two grama species regardless of the other species in the stand. Fewer stands were selected that had several grama species with low and intermediate abundances. This meant that stands often had zero values for a given grama species and therefore did not correlate well.

Regression Analysis and Habitat Factors Selections

Draper and Smith (1966) caution that step-wise multiple regression is sensitive and that independent variable selection must be carefully subjected to sensible judgement. Only the regression equations considered important for the stated purpose of studying variation are discussed. The variables are presented (Table 5) in order of selection and the number of variables is equivalent to the number of steps necessary to obtain those multiple correlation coefficients given. The factors selected do not necessarily agree with the product-moment correlation analysis, since the multiple regression analysis describes the relationship between a species and more than one variable.

Few habitat factors were found to be in common among the grama groups. Spruce-top, blue, and eludens grama were apparently more adapted to sandy soils, while spruce-top and hairy grama were more abundant on acidic soils. Steep slopes appeared to be a likely habitat for both eludens and sideoats grama; however, other factors varying between the species can be seen to be the ones really important in distinguishing the most favorable habitats of these two species.

The soils occupied by eludens and black grama were similar in that both were more abundant where potassium was less available and organic matter was high. Additional factors were noted that could be effective in distinguishing between the sites most often occupied by these two species (Table 5).

Partial Ordinations

Many of the relationships discovered by the correlation and regression analysis were also revealed by the ordinations; however, several new factors were indicated by the ordination methods. No attempt was made to compare the methods since the original intent was to only discover grama-environment and intergrama relationships. Ordinations using different combinations of factors resulted in defining the grama species interrelationships.

Species Ordination

Isolines based upon the maximum percent basal cover in the stand of one of the six most common grama species were drawn around stand locations (Fig. 1). The resulting groupings will be referred to as grama species groups. In this ordination, lines defining groups were least tortuous. We expected this since frequency and cover are vegetation indices that are usually correlated. While some of the other ordinations were better at defining some grama groups, this one was judged best for eliciting ecological relationships of all gramas and was chosen for more detailed analysis.

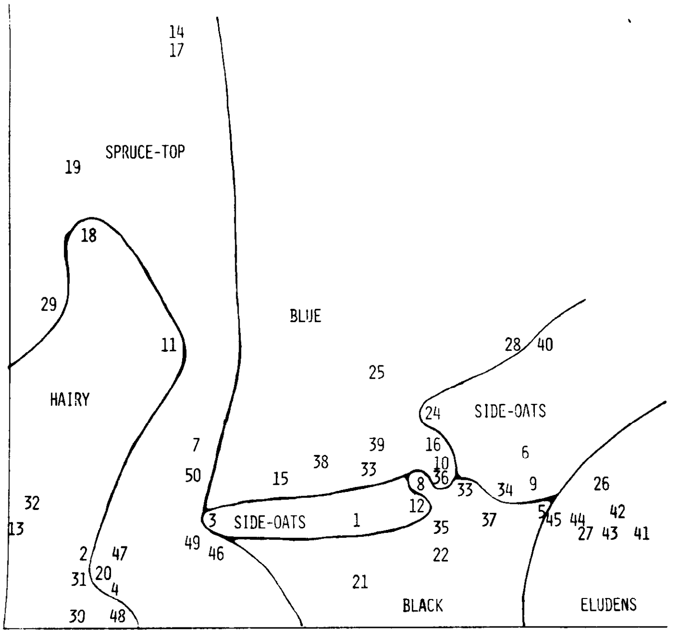

Fig. 1. *Location of stands on the two-axis partial ordination using plant frequency data only. Numerals are identification numbers.*

From left to right on the *x*-axis (Fig. 1) hairy grama (*Bouteloua hirsuta*) and spruce-top grama (*Bouteloua chondrosiodes*) show close association by virtue of their relatively close location. To the right, blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eriopoda*) are separated from sideoats grama (*Bouteloua curtipendula*) on axes representing continuity from one species to another in several directions but generally changing from left to right. Aggregated in the lower right corner are the eludens grama (*Bouteloua eludens*) stands.

The lines defining all groups represent in two dimensions the relative relationships of the grama species to one another with

Table 5. Results of stepwise multiple regression analysis. Variables chosen are those that were assumed to be most cognate in the habitats of the six gramas given. Each grama group was composed of the set of stands having the greatest percent basal cover for the said grama species.

	Grama species				
Spruce-top	Sideoats	Eludens	Black	Blue	Hairy
Elevation (+)	5–14 mm rock (+)	slope (+)	potassium (−)	15–30 mm rock (+)	pH (−)
% sand (+)	slope (+)	potassium (−)	organic matter (+)	% sand (+)	total species (−)
pH (−)	nitate (+)	organic matter (+)	nitrate (+)	>2 mm rock (−)	
Iron (−)	total species (+)	% sand (+)	zinc (−)	nitrate (−)	
R^*=0.80	R=0.84	R=0.70	R=0.90	R=0.71	R=0.63

* Multiple coefficient of correlation.

respect to total species composition and abundance in stands. Since there was little clumping of stands, we did not use ordination for reclassifying stand groups.

A simplified form of defining such intergrama relationship was used and judged more efficacious than plots of the stand numbers (Fig. 2). Lines connecting two species indicate proximity of stands on the ordination. Length of lines is proportional to the degree of overlap of stand locations.

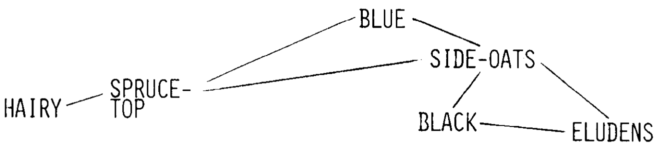

Fig. 2. *Diagram showing the general relationship of grama stands to one another based on the partial ordination in which plant species frequency data were used.*

Physical Factors Ordination

In the second ordination (Fig. 3) three groups exhibited considerable peripheral convolution; hairy grama divided both black and spruce-top grama stand locations. The behavior exhibited by the hairy grama stands, being very interspersed with these species stands, indicated that the levels of the measured physical habitat variables were similar. Conversely, within the eludens grama group, a tight homogenous pattern was exhibited, implying that physical habitat factor levels exhibited homogeneity. Eludens and blue grama were most different. The most likely physical factors associated with such patterns were those in which grama group means were most different (Table 1). The disparity of sideoats grama stands indicated probably adaptation to a wide variety of habitats. Its wide geographic distribution has been well documented by F. W. Gould and associates at Texas A&M University (Nicholson 1972).

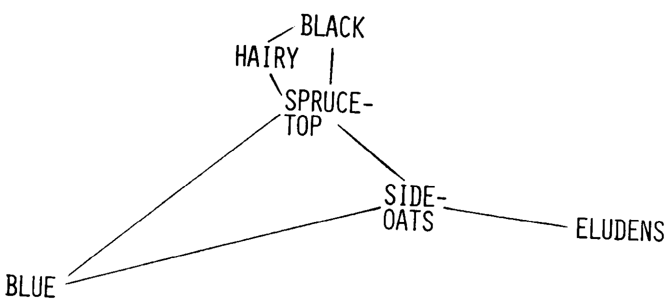

Fig. 3. *Diagram showing the general relationship of grama stands to one another based on the partial ordination in which physical factors of the soils were used.*

Chemical Factors Ordination

This ordination (Fig. 4) was effective in separating stands of eludens and black grama, indicating some degree of soil chemical uniqueness on the x-axis. Correlation analysis did not reveal this; however in the multiple regression, potassium and organic matter were two variables that each species had in common. Eludens grama stands were located quite close to spruce-top grama, whereas in other ordinations these two species are widely separated. The environments of these two species were more similar with regard to soil chemical factors than physical site factors and/or their related species.

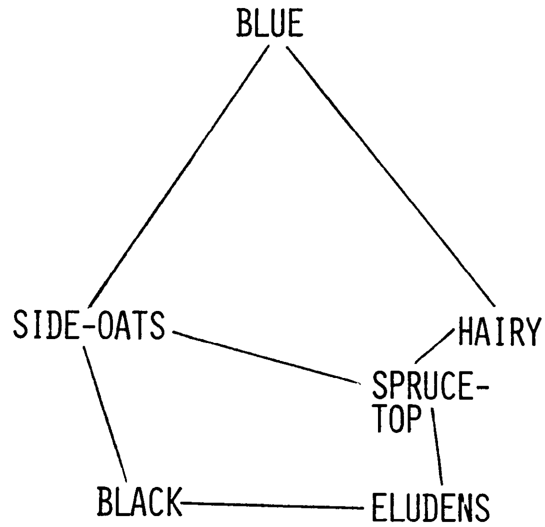

Fig. 4. *Diagram showing the general relationship of grama stands to one another based on the partial ordination in which chemical factors of the soils were used.*

Physical + Chemical Ordination

Combining physical and chemical factors in an ordination (Fig. 5) was an attempt to assess the total soil environment and its relationship with the gramas. Little additional insight was gained. Eludens grama stands retained their consistent relative homogeneity as in previous and subsequent ordinations, and hairy and sideoats grama stands remained mixed.

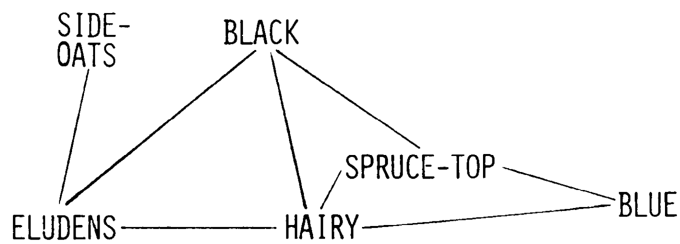

Fig. 5. *Diagram showing the general relationship of grama stands to one another based on the partial ordination in which both physical and chemical factors were used.*

Species + Physical + Chemical Ordination

The ordination in which all three types of data were combined (Fig. 6) exhibited more discernible stand groups than the previous combinations. This apparently was due to the inclusion of frequency data, since the resulting locations of the stand groups were similar to the frequency ordination. This is probably the best overall depiction of the ecological intergrama relationships. Hairy and spruce-top were intimately related and unique with some spruce-top stands being similar to blue and sideoats but not to black grama. However, black grama stands were more similar to sideoats grama than blue or spruce-top grama. Sideoats grama stands were in turn most similar to eludens grama.

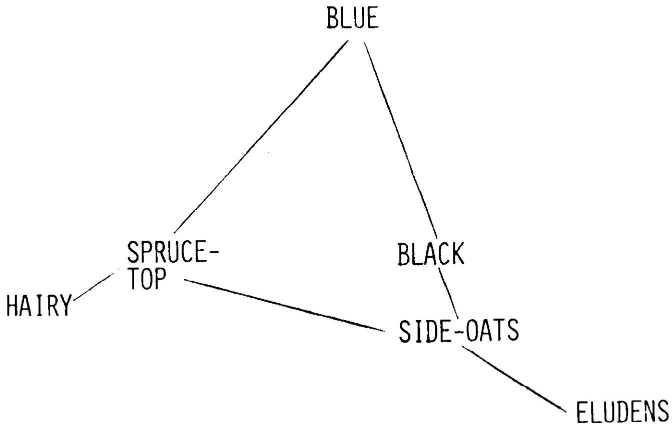

Fig. 6. *Diagram showing the general relationship of grama stands to one another based on the partial ordination in which all factors and plant frequency were used.*

Variables Plotted on Species Ordination

Values of habitat variables (physical, chemical, and species) were plotted directly on the stand positions of the two dimensional *species* ordination graph (Fig. 1) as described earlier. A total of 43 of such graphs were prepared. Isolines were drawn on each graph to separate stands in which variables have similar or equivalent value. By inspecting these 43 graphs, we discerned the variables that showed trends with respect to the ordination axes. Most in-group variation was best indexed by noting the relative degree of tortuosity of the isolines. One of the 16 physical factor graphs is presented to demonstrate the procedure (Fig. 7).

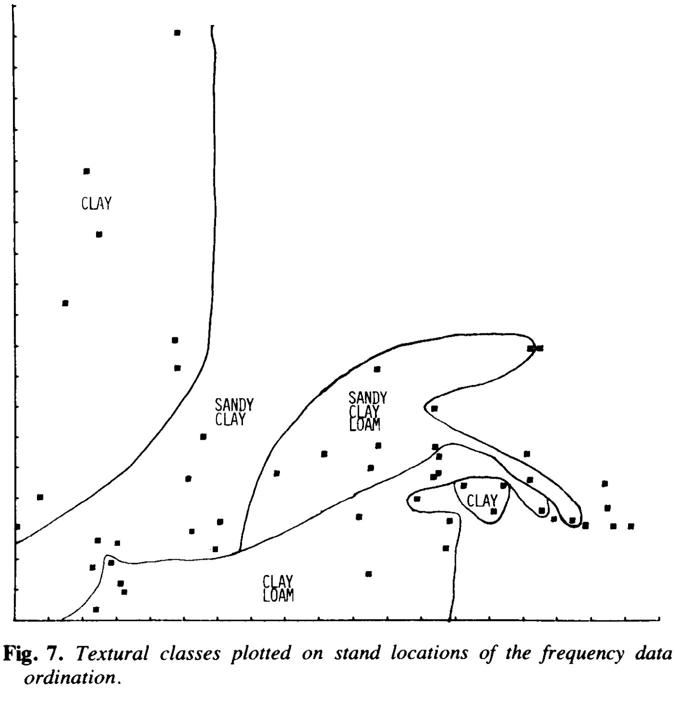

Fig. 7. *Textural classes plotted on stand locations of the frequency data ordination.*

Physical Factor Plots

The effects of soil texture is best summarized by noting the gradation from the clay class (upper left) to clay loam class (lower center), between which are the sandier classes of soils. It was informative to relate positions of maximum percent basal cover of the grama species (Fig. 1) to the positions of the textural classes on the same ordination (Fig. 7). Eludens grama stands were all in the same position as the sandy clay class, and blue grama stands were all classed as sandy clay loams. Sideoats grama did not occur abundantly on clay soils, and the other gramas showed no clear-cut association with any textural class. A similar procedure was followed thenceforth to discover additional associations between grama species and habitat and between grama species and associated species.

Rock content of the upper soil surface is probably best overall indexed as the total rock fraction (all rocks greater than 2 mm). Stands with low rock content in all classes seemed to be somewhat centered on the ordination surface, while stands of higher rock content were distributed in the periphery. By comparing the plotted values of the >2-mm rock on the frequency ordination with the grama stand groups, we found that the blue grama stands appeared to be associated with the low rock content. Few discernible trends were observed in the other stand groups and most showed variable responses. However, eludens grama stands consistently were located in the region of the ordination of higher surface rock in all size classes.

Responses of species were somewhat variable with respect to the percent soil water at the three levels of soil water stress. It appeared that black, hairy, and spruce-top grama were associated with moderate to high values, eludens and sideoats grama with moderate values, and blue grama with low values.

Slope was another variable in which the highest values were centered. Eludens grama stands were consistently found on steeper slopes in addition to the fact that none of these stands had any northern exposure. Also notable was the fact that all but one of the spruce-top grama stands were located at higher elevations and this was the only habitat factor that showed any consequential association with this species. Blue grama stands were mostly northern exposures.

Chemical Factor Plots

Eludens, hairy, and sideoats stand group soils generally tended to be alkaline and higher in lime, while the soils under the remaining three species were lower in lime and acidic. Soils of blue grama stands were mostly low in organic matter while soils of spruce-top, hairy, black, and eludens grama stands had generally higher values. Potassium was probably more available in black and eludens grama soils, while in the soils under blue and hairy grama potassium was less available. The exact reverse situation was found to be the case with iron and zinc availability. In addition, zinc tended to be more available under high cover of spruce-top and sideoats grama.

Nitrate-nitrogen levels were lower in stands predominantly covered by blue grama and eludens grama. The reciprocal of this was true with respect to stands with highest cover values of black grama.

Species Plots

Some of the gramas tended to occur consistently with certain species. These kinds of interspecies associations were determined utilizing the ordination isoline comparison method previously described regarding grama-habitat relationships.

Inferences made from these comparisons were made only on the order of which species one might expect to occur *abundantly* with the *abundant* occurrence of a species of grama, or which species one would *not* expect to occur abundantly with abundant occurrences of a grama. The advantage of this method was that zero frequency values could be interpreted as ecologically meaningful, while in the interspecific correlation analysis zeros do not convey any information.

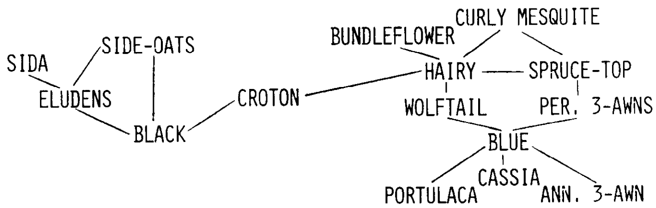

Fig. 8. *Diagram representing interspecies relationships derived from multiple stepwise regression.*

The interspecific associations so determined were summarized in a matrix. A two-space picture appeared to be the best method of presentation of these results (Fig. 8). The general pattern of intergrama relationships is similar to that determined from the different types of ordinations, especially the all-factors ordination (Fig. 6). The most important species in the stands in addition to the gramas are shown with respective associations. The length of lines connecting species is only roughly proportional to the intensity of the interspecies association.

Conclusions

The initial intent of this research was to describe the habitats of six grama species in an area of southern Arizona. Gramas were chosen because of the large number of species and the importance of these species as range plants.

The following descriptions of grama community structure were found. Environmental factors that were not mentioned exhibited continuous variation within and among the groups to the extent that categorical generalizations were not feasible.

1. Black grama: Relatively larger amounts of available nitrate, available potassium, and/or organic matter distinguished the habitat associated with this species. Soil water percentages at the various water potentials were high. Most of these soils were also high in pH and/or lime. Coryumbed croton (*Croton corymbulosis*) was found consistently on these sites. Black grama stands were most similar to eludens and sideoats grama stands.

2. Blue grama: Soils associated with this species were found to be low in pH, available nitrate, potassium, and/or rock. They were sandy, consequently low soil water percentages were found at all levels of induced stress. Portulaca (*Portulaca parvula*), partridge pea (*Cassia leptadenia*), wolftail (*Lycurus phleoides*), perennial threeawns (*Aristida* species), and annual threeawn (*Aristida adscensionis*) were commonly associated species. Blue grama habitats were considered relatively unique and not well associated with other grama species.

3. Eludens gama: Light textured soils, steep, and/or rocky slopes were commonly associated. Sites were much drier than the sideoats grama stands, mostly because eludens grama stands were all southern exposures. Soils occupied were more alkaline than those of sideoats grama, high in organic matter, relatively lower in available nitrate, and/or higher in available potassium. Available soil water was low. Stands in this group were most uniform of any, not only with regard to the physical-chemical habitat but also associated species. Coryumbed croton, sida (*Sida procumbens*), black and sideoats grama were consistently found in the eludens grama stands.

4. Hairy grama: Sites associated were relatively flat with soils that were low in potassium and/or acidic. These stands were most similar to spruce-top grama. Percent soil water at 0, ⅓, and 15 bars induced stress was generally high. Stands were species poor, yet had a large number of species which were characteristically associated: perennial threeawns, wolftail, bundle flower (*Desmanthus cooleyi*), and curly mesquite (*Hilaria belangeri*).

5. Sideoats grama: Steep and rocky slopes were characteristic of the environment of the species. Associated soils were generally alkaline, relatively high in available nitrate, and low in available water percentages. Species richness characterized most of these stands, yet no individual species was found to be associated with sideoats grama.

6. Spruce-top grama: An abundance of this species was found on shallow slopes and/or the higher elevations, nearly always mixed with hairy grama. Soils associated with this species were low in pH (acidic), clay in texture, and therefore able to maintain fairly high percentages through the ranges of soil water potential. Species commonly associated were the threeawns and curly mesquite.

Structural descriptions are a necessary first stage in ecosystem analysis. Structural hypotheses formulated, tested, and found to be statistically significant can lead to the formulation of functional hypotheses, which in turn can be tested. Such procedures lead to the knowledge requisite for learning how range ecosystems are organized and function. In turn, fundamental knowledge of range ecosystems is a prerequisite to wise and fruitful management.

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